Received: 29 May 2019 | Revised: 7 February 2020 | Accepted: 15 February 2020

DOI: 10.1111/gcb.15063

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Habitat patchiness, ecological connectivity and the uneven recovery of boreal stream ecosystems from an experimental drought

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Funding information
Swedish Environmental Protection Agency; Swedish Agency for Marine and Water Management, Grant/Award Number: Dnr 10/179; Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning, Grant/Award Number: Dnr 2014-886; Department of Aquatic Sciences and Assessment; University of Oulu Graduate School; Academy of Finland; Natural Resources Institute Finland

Abstract

Ongoing climate change is increasing the occurrence and intensity of drought episodes worldwide, including in boreal regions not previously regarded as drought prone, and where the impacts of drought remain poorly understood. Ecological connectivity is one factor that might influence community structure and ecosystem functioning post-drought, by facilitating the recovery of sensitive species via dispersal at both local (e.g. a nearby habitat patch) and regional (from other systems within the same region) scales. In an outdoor mesocosm experiment, we investigated how impacts of drought on boreal stream ecosystems are altered by the spatial arrangement of local habitat patches within stream channels, and variation in ecological connectivity with a regional species pool. We measured basal ecosystem processes underlying carbon and nutrient cycling: (a) algal biomass accrual; (b) microbial respiration; and (c) decomposition of organic matter, and sampled communities of aquatic fungi and benthic invertebrates. An 8-day drought event had strong impacts on both community structure and ecosystem functioning, including algal accrual, leaf decomposition and microbial respiration, with many of these impacts persisting even after water levels had been restored for 3.5 weeks. Enhanced connectivity with the regional species pool and increased aggregation of habitat patches also affected multiple response variables, especially those associated with microbes, and in some cases reduced the effects of drought to a small extent. This indicates that spatial processes might play a role in the resilience of communities and ecosystem functioning, given enough time. These effects were however insufficient to facilitate significant recovery in algal growth before seasonal dieback began in autumn. The limited resilience of ecosystem functioning in our experiment suggests that even short-term droughts can have extended consequences for stream ecosystems in the world's vast boreal region, and especially on the ecosystem processes and services mediated by algal biofilms.

KEYWORDS
algal production, detritivores, drought, ecosystem processes, habitat patch, hyphomycete fungi, meta-ecosystem, spatial connectivity

1 | INTRODUCTION

The ecological impacts of drought have gained growing attention over the last decade as drying events increase in intensity and frequency worldwide due to climate change, including in regions not previously regarded as drought prone (ACIA, 2005; Wang, Hogg, Price, Edwards, & Williamson, 2014). This includes the vast boreal region, where a historical pattern of short-term drying events with a patchy landscape level impact are expected to shift towards a greater frequency of longer term droughts acting at larger, regional scales (ACIA, 2005; Hannaford, Lloyd-Hughes, Keef, Parry, & Prudhomme, 2011; Spinoni, Vogt, Naumann, Barbosa, & Dosio, 2018). The boreal region is the world's second largest forested biome, and contains the world's largest standing stocks of surface freshwater, supports unique biodiversity and plays key roles in global carbon (C) cycling and climate regulation (Baldocchi, Kelliher, Black, & Jarvis, 2000; Bradshaw & Warkentin, 2015; Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015). Unfortunately, our current empirical basis for understanding and projecting impacts of drought on the biodiversity and ecosystem functions supported by boreal ecosystems is very limited, reflecting the overwhelming focus of most drought research on arid, semi-arid and Mediterranean ecosystems (Acuña et al., 2005; Bogan, Boersma, & Lytle, 2015; but see Brown, Dickson, Carrivick, & Füreder, 2015; Chapin, Oswood, Van Cleve, Viereck, & Verbyla, 2006).

Droughts are viewed as 'ramp' disturbances (Lake, 2000) that gradually reduce water availability to extremely low levels for an extended time. Terrestrial and aquatic environments dry not only as a consequence of larger scale climatic variation, but also from the local-to-regional scale impacts of water abstraction and river regulation, deforestation and afforestation (Göthe et al., 2019; IPCC, 2014; Jackson et al., 2005; Malmqvist & Rundle, 2002; Van Loon & Van Lanen, 2013). Indeed, broad-scale models predict an intensification of groundwater depletion driven both by increased human water demands and climate change, coupled to an increase in the frequency and magnitude of water abstraction and drought (Dankers & Feyen, 2008; IPCC, 2014; Taylor et al., 2012). Apart from strong direct effects on the availability and quality of water, drought also affects food resources, key habitats (Acuña & Tockner, 2010; Lake, 2003; Schimel, 2018) and community composition and diversity (Ochoa-Hueso et al., 2018; Sarremejane et al., 2018; Schimel, 2018). These effects often have further consequences, not only for the densities and size (or age) structure of populations (Lake, 2003; Ochoa-Hueso et al., 2018; Schimel, 2018), but also for trophic pathways and interactions, and ecological connectivity both within habitats, and across habitat boundaries (Carson et al., 2010; Stanley, Fisher, & Grimm, 1997).

Natural flowing rivers have four axes of hydrological connectivity (Pringle, 2001; Stanford & Ward, 1993): longitudinal, vertical, lateral and temporal, which apply to water, dissolved and particulate materials, and biota. Drought disrupts these connections, with shallow habitats (i.e. riffles) typically being the first to disappear, resulting in a series of longitudinally disconnected pools (Larned, Datry, Arscott, & Tockner, 2010; Stanley et al., 1997). Over time, lateral (stream-riparian) and vertical (surface-groundwater) links are weakened as wetted habitats disappear (Lake, 2003), with profound impacts on biodiversity and ecosystem functioning, which often persist after the drought has ended (Lake, 2000). The longer term persistence of these impacts depend on key aspects of ecosystem stability (Donohue et al., 2013), including: (a) the ecosystem's capacity to first buffer the impacts of drought (resistance); and (b) the ecosystem's speed of recovery towards pre-disturbance levels (in line with the concepts of 'engineering resilience' or 'elasticity'; Boulton, 2003; Holling, 1973).

The hydromorphological dynamism of streams generates substantial patchiness in the distribution of key habitats (e.g. rocky substrates) and resources (e.g. detritus) within individual channels, with individual resource patches further varying greatly in size (e.g. Hoover, Richardson, & Yonemitsu, 2006). Connectivity among those habitat patches or among ecosystem compartments (e.g. different reaches in a stream network) can contribute to ecological stability during and after environmental disturbances (Allen et al., 2016; Elmqvist et al., 2003; Loreau et al., 2002). For example, survival and subsequent recovery by stream microbial and invertebrate assemblages during and after drought is facilitated by the use of wetted refuges during the drying period (Bogan et al., 2015; Carson et al., 2010), and poor connectivity within a stream network may restrict the potential for biota to recolonize from these refuges post-disturbance. At larger scales, ecological connectivity might favour the maintenance and recovery of biodiversity and ecosystem functioning during and after disturbances (Elmqvist et al., 2003; Leibold et al., 2004; Peterson, Allen, & Holling, 1998) if dispersal from the regional species pool facilitates the recovery and/or replacement of sensitive species by more tolerant taxa (sensu the insurance effect hypothesis; Yachi & Loreau, 1999). In boreal regions, spatial processes explain at least as much variation in ecosystem functioning as local environmental variation and community composition (Truchy et al., 2019). Presently, prediction of drought effects on stream food webs is limited by our understanding of how connectivity among habitat patches regulates the stability of biodiversity and ecosystem functioning from local to regional scales.

We investigated the impacts of drought on boreal stream communities and ecosystem functioning, and how those effects are altered by variation in ecological connectivity and habitat patchiness in an experiment conducted in flow-through stream

mesocosms. We focussed on two ecosystem processes underlying C and nutrient cycling in streams: (a) decomposition of organic matter, quantified with the aid of standard leaf litter and cotton-strip assays; and (b) algal biomass accrual on inorganic substrates. We focussed on two organism groups dependent on allochthonous detritus—hyphomycete fungi and leaf-eating invertebrates—and characterized functional feeding groups in benthic invertebrate communities. Compared to the macroconsumer responses described above, spatial mechanisms structuring microbial communities have proven more challenging to understand (Kivlin, Winston, Goulden, & Treseder, 2014; Matthiessen, Gamfeldt, Jonsson, & Hillebrand, 2007; Tedersoo et al., 2014), although propagules are known to disperse by both water- and wind-borne pathways, with the latter especially important after drought (Bärlocher, 2009; Chauvet, Cornut, Sridhar, Selosse, & Bärlocher, 2016). This is a key shortcoming, given the fundamental roles microbes play in both terrestrial and aquatic ecosystems, for example driving decomposition and contributing to the cycling of C and nutrients (Baldrian, 2017; Bärlocher, 1992a). We hypothesized that drought has overall negative effects on both structural and functional properties of streams, and that drought resistance and recovery differs among organism groups and the ecosystem processes they mediate, reflecting the different spatiotemporal scales over which each organism group operates. Finally, we expected that greater spatial proximity of habitat patches within channels and enhanced connectivity with a regional species pool generally favour faster recovery of organism groups and ecosystem processes.

2 | MATERIALS AND METHODS

2.1 | Experimental setup: Artificial stream channels

We manipulated flow, spatial arrangement of resources and ecological connectivity in flow-through artificial stream channels (Figure 1) in an experiment conducted for 6 weeks from 19 August to 9 October 2015 (Figure 2). The artificial channels are maintained outdoors at the Natural Resources Institute Finland, adjacent to the free-flowing Varisjoki River (aerial distance: ~300 m) in the boreal region of northern Finland. Water is drained from the nearby Lake Kivesjärvi via pipelines into a 300 m^2 pond located in the research station; it then enters a 30-m long, permanently flowing stream channel (the proximate source of colonizing organisms) before draining into the experimental channels. Water flowing through the experimental channels was nutrient poor (total phosphorus: 17.8 ± 2.5 µg/L; total nitrogen: 390 ± 49 µg/L). Streambeds in the channels consisted of a 0.2–0.3 m thick layer of gravel and cobbles. Invertebrate communities found in the channels were similar to those in the nearby Varisjoki River (both in terms of species composition and densities; Turunen et al., 2018). Five days prior to the commencement of our experiment, four instream subchannels (constructed from rustproof metal gutters, 0.20 m wide and 6 m long) were placed within each of the six main experimental whole channels (Figures 1 and 2), and filled with substrate similar to that of the main experimental whole channels. This resulted in 24 experimental units, which constitute the replicates to which our different treatment combinations were applied.

2.2 | Experimental treatments

Our experimental treatments were applied to our main and subchannel sampling units in a 'split-plot' design (Figure 1). Two levels of flow (constant flow vs. drought) were applied to the main channels, while the two levels of habitat patchiness (aggregated vs. evenly spaced habitat) and two levels of connectivity to a regional species pool (ambient connectivity vs. enhanced connectivity) were applied to the subchannels nested within the main channels. These treatments are detailed below.

2.3 | Detrital resources and habitat patchiness treatment

We manipulated the spatial arrangement of heterotrophic resources (Figure 1), comprising leaf litter and cotton strips, and serving as both habitat and detrital resource for invertebrates and fungi. The habitat patchiness treatment comprised two levels: *aggregated* and *evenly spaced* (Figure 1). In the aggregated habitat treatment, 10 litterbags were arranged in two larger groups of five each (Figure 1), at the beginning and end of each subchannel, with five cotton strips buried in the sediments under each litterbag aggregation. For the even distribution treatment, the 10 litterbags and cotton strip sets were spaced at regular 0.5 m intervals. This distance is in the same order of magnitude as that between litterbags in the study by Presa Abós, Lepori, McKie, and Malmqvist (2006), who found significant spatial structuring of boreal leaf-eating invertebrate communities over this spatial scale. The habitat patchiness treatments were established on day 0 of the experiment (August 24; Figure 2).

2.4 | Drought treatment

On day 0, water flow was equalized at the whole-channel scale using a channel-specific valve system. For our drought treatment, we reduced discharge on day 17 of the experiment (Figure 2) in three whole channels (affecting 12 subchannels in total) from a mean discharge of 5.5 ± 0.01 L/s until only a trickle of water flowed through the substrate (Figures 1 and 2). There was no manipulation of discharge in the remaining 12 subchannels during this period, which constituted controls for the drought treatment. After 8 days of drying (day 24; Figure 2), discharge in the drought-affected channels was returned to that of the controls, ensuring a sufficient time post-drought to assess ecological recovery before the onset of ice formation in the autumn. Discharge was not further manipulated for the remainder of the experiment. The duration of the drought treatment and the extent of flow reduction mimic low water event which might

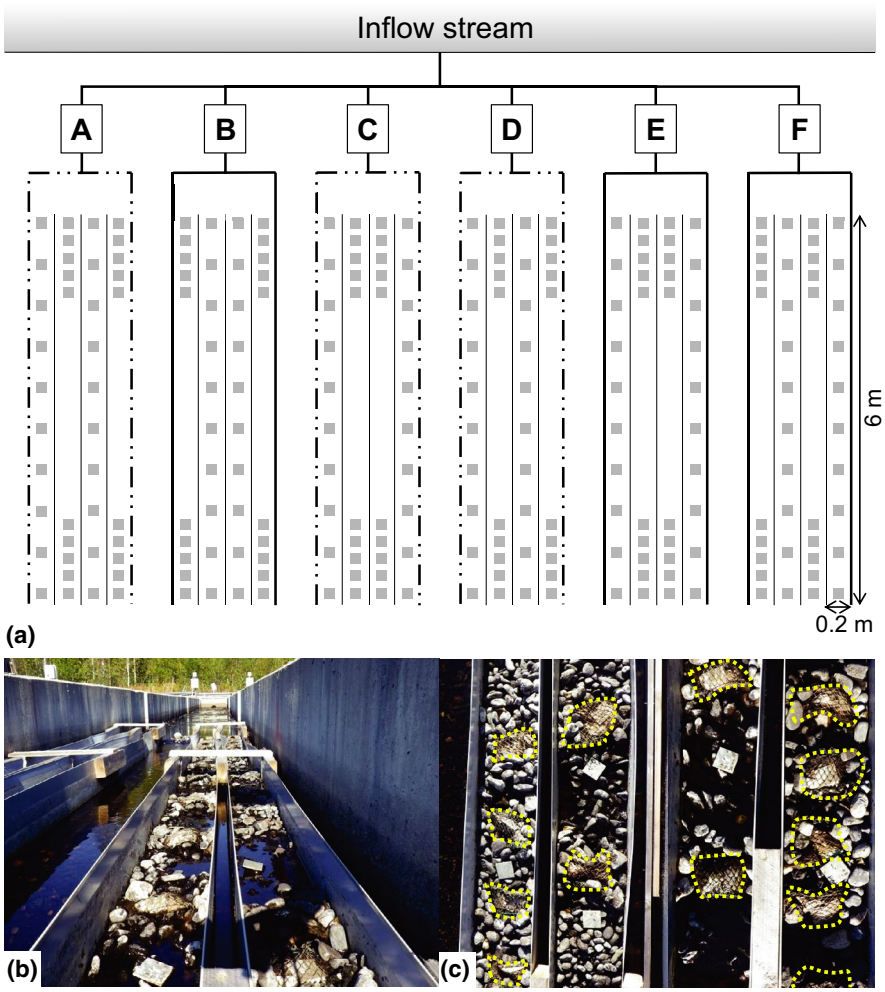

FIGURE 1 Experimental design (panel a) and subchannels photographed during the drought treatment (panels b and c). Panel (a) is a schematic representation of the experimental design showing the six main channels with independent inflows (A–F), each containing four subchannels. The drought treatment was applied at the whole-channel scale, with three randomly allocated to drought (dotted line) and three left as controls (plain lines). These channels were not completely dry, as water flowed through the sediments and accumulated in small pools. Habitat patchiness and enhanced connectivity treatments were applied to subchannels nested within whole channels. The habitat patchiness treatment was achieved by varying the spatial arrangement of litterbags (grey squares in panel (a) and yellow-dotted lines in panel (c)) which were either aggregated at each end of the subchannel or evenly spaced along the subchannel. Enhanced connectivity was achieved by adding invertebrates, collected from the nearby Varisjoki River, in 12 subchannels (black arrows). Each patchiness × connectivity treatment combination was randomly allocated to one of the subchannels within each whole channel

arise as a result of late summer drought, water abstraction or river regulation associated with hydropower.

2.5 | Enhanced connectivity treatment

On day 24 (Figure 2), after the drought treatment concluded, we added benthic invertebrates to 12 subchannels to simulate enhanced connectivity with a regional species pool (Figure 1). This experimental manipulation aimed to simulate increased rates of movement for both stronger and weaker dispersing taxa, as might occur following an increase in discharge which disturbs substrates and transports a wider array of taxa than those dominating drift at base flow, without overly increasing mortality (Lepori & Malmqvist, 2009; Sponseller, Heffernan, & Fisher, 2013). Invertebrates were obtained from the adjacent Varisjoki River by kick-net sampling (mesh size: 500 μm) for 2 min. These samples were obtained prior to autumn litter fall and the subsequent build-up of extensive leaf packs. However, the samples did encompass extensive patches of mosses growing on rocky substrates, known to harbour both leaf-shredder and other invertebrate feeding groups (Muotka & Laasonen, 2002). Invertebrates were separated from substrate and mosses, ensuring no additional coarse substrata were added to the subchannels. Accordingly, the samples added to the channels comprised of new invertebrate individuals, plus any fine particulate organic matter (FPOM), sediments or microorganisms that might have been transported with the invertebrates (i.e. attached to their bodies or within their digestive tracts), or in residual water from the source stream. We then distributed collected invertebrates homogeneously along the upper half of each subchannel. Four extra kick

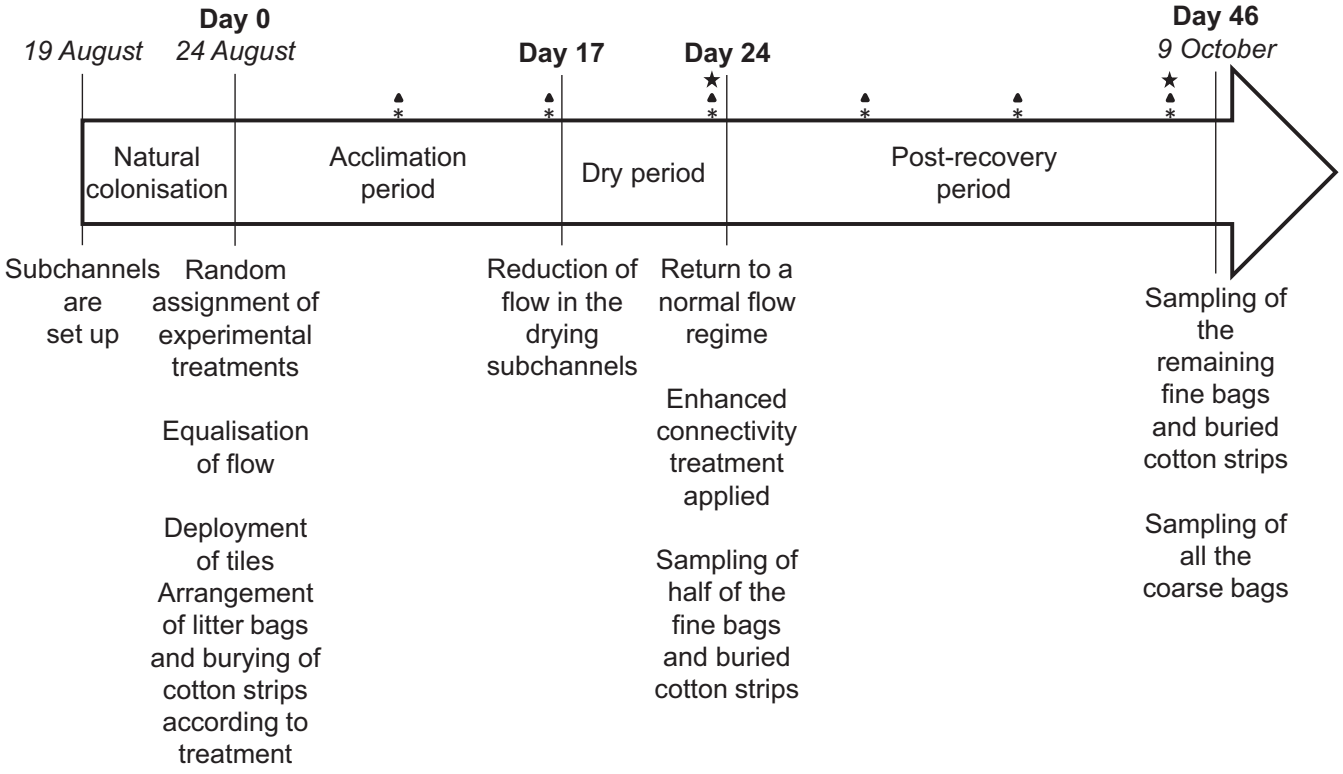

FIGURE 2 Timeline covering both the acclimation and 6-week experimental period, with key experimental steps and sampling occasions identified. The acclimation phase lasted 2 weeks, the drought-treatment channels were dried for 1 week and we allowed for slightly over 3 weeks of recovery. Triangles indicate the sampling points for algal biomass measurements, asterisks are flow measurements and stars represent the benthic invertebrate samplings within the experiment subchannels

samples were collected to identify the invertebrates and estimate densities added to the experimental units (Table S1.2).

2.6 | Physico-chemical measurements during the experiment

We measured flow velocity on eight dates at four random locations per subchannel, using a MiniAir 20 flowmeter (Schiltknecht). From these velocity data, we calculated the mean discharge (L/s) per unit cross-sectional area of the channels.

Whole-channel water temperatures were recorded continuously during the experiment using data loggers buried shallowly in the substrate (SL5x; Signatrol). We used these records to calculate sum of degree days above zero. Water conductivity, turbidity, oxygen saturation, pH and chlorophyll *a* concentration were recorded weekly in each whole channel (i.e. seven occasions in total) using a MANTA multiparameter water quality probe (Eureka Environmental Engineering).

2.7 | Functional response variables

We quantified four metrics representing ecosystem functioning: algal biomass accrual, organic matter decomposition (leaf litter and cotton strips), the biomass of hyphomycete fungi and the respiration of heterotrophic microbes.

To quantify algal biomass accrual, we deployed 10 unglazed bathroom tiles (50 × 50 mm) evenly spaced onto the substrate of each subchannel on day 0 (Figure 2). Once per week (6 weeks in total; Figure 2), we quantified algal standing stocks using a Benthotorch (bbe Moldaenke Gmbh), with three readings per tile. The Benthotorch measures and converts fluorescence of chlorophyll *a* into an estimate of chlorophyll biomass that is comparable to that derived from more traditional chlorophyll extraction procedures (Kahlert & McKie, 2014). The standing stock of chlorophyll *a* was expressed as mg/m^2. One set of Benthotorch measurements was taken from dry tiles in drought-affected channels. According to the manufacturer (https://www.bbe-moldaenke.de/en/knowledge-media), measurements from dry substrates are within the Benthotorch's capabilities, but are likely to be less accurate than readings from wet substrates. In our study, the measures of chlorophyll *a* biomass from the drought-affected tiles were extremely and uniformly low both when dry and when rewet 1 week later (see Section 3).

We quantified organic matter decomposition by assessing mass loss of litter in coarse and fine bags, and the loss of tensile strength of cellulose (cotton) strips. Air-dried silver birch leaves (*Betula pendula* Roth), collected at abscission, were deployed in 10 coarse bags (mesh size = 10 mm) in each subchannel, with each containing 3.0 ± 0.1 g of litter. This mesh size was sufficient to allow access to

the litter by both leaf-eating invertebrates and microbial decomposers. Associated with each coarse bag were one fine bag containing leaf litter and two cotton strips, all deployed to allow more specific assays of microbial activity over multiple retrieval dates (see below). The fine bags consisted of tetrahedron-shaped tea bags (Lipton®; Unilever) made of biodegradable plastic filled with 0.02 ± 0.001 g of birch litter, with a mesh size (ø = 0.25 mm) that allows access for microorganisms while excluding larger leaf-eating invertebrates. Cotton strips are used as a highly standardized assay for quantifying the decomposition activity of microbial decomposers, measured as the loss in strip tensile strength following exposure in the aquatic environment (Tiegs, Clapcott, Griffiths, & Boulton, 2013). Our strips were cut from woven artist canvas (universal Claessens), with each strip 80 × 25 mm in area. The strips were first leached under running tap water for 24 hr to remove any residual chemicals from the manufacturing process, oven-dried and then weighed to the nearest 0.01 g prior to deployment. The coarse bags (each containing litter and a cotton strip) and the fine bags were placed on the substrate of the subchannels, while the remaining cotton strips were buried in the substrate (depth≈80 mm). The coarse bags were retrieved at the end of the experiment, after the post-recovery period (Figure 2). Cotton strips and fine bags were retrieved on two occasions: half of the fine bags and cotton strips were retrieved just after drought release (day 24; Figure 2) while the other half stayed in until the end of the post-recovery period (Figure 2).

After retrieval of coarse bags, we rinsed all leaves with tap water to remove colonizing invertebrates, which were preserved in 70% ethanol for later identification. Two sets of five 12 mm diameter leaf discs each were cut from five different leaves from each coarse bag, for later ergosterol and DNA analyses (see below). All leaves were subsequently oven-dried for 48 hr at 110°C, weighed to the nearest 0.001 g and then ashed at 550°C for 4 hr to obtain ash-free dry mass. Leaf mass loss was corrected for leaching losses (determined with a 24 hr laboratory trial) and the breakdown rate coefficient *k* was calculated for each litterbag based on the negative exponential decay model (Benfield, 1996).

To further characterize variation in the activity of heterotrophic microbes, we quantified respiration rates of biofilm associated with both cotton strips (those enclosed in the coarse bags and those buried in the sediments) and litter from the fine bags, using a modified version of the dark bottle method (Johnson, Tank, & Dodds, 2009). Respiration rates were measured on two occasions: immediately post-drought and again at the termination of the experiment. Cotton strips or leaves were placed in 80 ml containers filled with unfiltered but oxygen-saturated channel water. Each container was sealed with transparent Parafilm M® (Bemis) and incubated in the dark for 3 hr. Five additional containers per whole channel were filled with water only to correct for background variation in dissolved O_2 during the incubation. After 3 hr, dissolved O_2 was measured using optical sensors (FireString O_2; Pyro Science), and corrected for water temperature and surrounding atmospheric pressure. Microbial respiration was then calculated as the difference in O_2 between the start and end of the incubation, corrected for background O_2, volume of the container and dry weight of leaves or cotton strip (as $\mu g\ O_2\ mg^{-1}\ hr^{-1}$ consumed).

After the respiration measurements, leaves from the fine bags were rinsed, oven-dried for 48 hr at 110°C and weighed to the nearest 0.001 g. The cotton strips were placed separately in a tray containing 80% ethanol for 30 s, to end microbial activity and prevent further degradation. The cotton strips were then dried at 40°C for 48 hr and weighed to the nearest 0.01 g. To measure tensile strength, cotton strips were mounted in a tensiometer (Mark-10; Series 5, Force gauge model M5-100). The strips were pulled apart with the aid of a motorized test stand at a fixed speed of 2 cm/min and the maximum tensile strength recorded. Tensile loss was expressed as percent of the initial tensile strength lost per day (Tiegs et al., 2013).

2.8 | Biota on the litterbags

We quantified fungal community composition on the second set of leaf discs cut from the coarse litterbags using next generation DNA sequencing (six litterbags per subchannel). Freeze-dried leaf discs were pulverized and fungal DNA was extracted from 0.07 g of leaf material using a PowerSoil DNA Isolation Kit (MO BIO laboratories). Each fungal DNA sample was diluted to 5 ng/µl and the rRNA coding regions were amplified using internal transcribed spacer (ITS) primer ITS1F (Gardes & Bruns, 1993) and R-primer 58A2R (Martin & Rygiewicz, 2005). Amplicons were sequenced using the Ion Torrent Personal Genome Machine™ sequencer at Biocenter Oulu Sequencing Center (University of Oulu, Oulu, Finland) with Ion HiQ chemistry and 316 chips (see Lehosmaa et al., 2018). All sequences were analysed using the Quantitative Insights into Microbial Ecology pipeline (Caporaso et al., 2010). The sequence library was split by samples and a quality filter based on quality scores for every sequence. Minimum and maximum sequence lengths were set to 200 and 1,000 bp respectively. Quality scores below 25 and sequences with more than two mismatches in the primer were also removed. Sequences were clustered into operational taxonomic units (OTUs) using the Usearch61 algorithm, clustering OTUs at 97% identity (Edgar, 2010). Chimeric OTUs were detected using the UNITE database (Kõljalg et al., 2013) and removed from further analyses, as were rare OTUs occurring in <10 samples (initial number of OTUs: n = 13,128). Taxonomical assignment of OTUs was performed using the BLAST (basic local alignment search tool) database of NCBI (National Center for Biotechnology Information, USA) GenBank's non-redundant nucleotide. Since sequence number varied among samples, sequences were rarefied to the lowest shared sample size (n = 8,037) to ensure equal sampling depth. We further eliminated rare taxa occurring in <1% of the samples.

Leaf-eating detritivores, representing a functional feeding group known as 'shredders' (defined as Cummins, 1974) colonizing the coarse bags were identified to the lowest taxonomic level possible (generally species, but genus for *Tipula* sp. [Diptera] and for small individuals of *Nemoura* sp. [Plecoptera]).

2.9 | Fungal and leaf-shredding invertebrate biomass

We quantified fungal biomass on the leaf discs from the coarse bags (four litterbags per subchannel), using a modified ergosterol assay (Wallander & Nylund, 1992). The leaf discs were first freeze-dried, and then ergosterol extracts were quantified with high-pressure liquid chromatography using a reverse-phase C18 column equipped with a pre-cartridge and methanol as the eluent (1.0 ml/min, column temperature 30°C). Leaf discs were pooled at the subchannel scale to ensure extraction of sufficient ergosterol for analysis. Commercial ergosterol (5,7,22-ergostatrien-3ß-ol; Fluka AG) was used as standard. Results are expressed as ergosterol concentration (µg/g) in dry litter weight.

We measured the body length of leaf-shredding invertebrates to the nearest mm, which were used to estimate shredder biomasses using the published regressions of Baumgärtner and Rothhaupt (2003) and Meyer (1989).

2.10 | Benthic invertebrates

Benthic communities in experimental channels were sampled on two occasions (Figure 2): immediately post-drought but before the application of the enhanced connectivity treatment; and at the experiment's termination. Invertebrates were collected using a Surber sampler (200 × 200 mm, 0.5-mm mesh size) at 1, 3 and 5 m from the downstream end of the subchannels. The samples were washed through a 0.5-mm sieve, with retained invertebrates preserved in 70% ethanol. In the laboratory, invertebrates were sorted and identified to the lowest taxonomic level possible (generally species, but family for Chironomidae, Simuliidae and Ceratopogonidae [all Diptera], small limnephilid caddisflies [Trichoptera] and Corixidae [Hemiptera]).

Here, data from these benthic samples are used primarily to assess how variation in ecosystem processes might relate to fluctuations in the dominant feeding traits characterizing invertebrate assemblages which— in line with Grime's Mass Ratio Hypothesis (Grime, 1998)—are most likely to influence functioning. To achieve this, we first extracted information on the 'functional feeding traits' characterizing invertebrates in our benthic samples from Tachet, Bournaud, Richoux, and Usseglio-Polatera (2010). Species were scored according to their affinities for five feeding trait categories: predators, algal biofilm scrapers, leaf shredders, filterers (consuming suspended FPOM) and deposit feeders (consuming deposited FPOM). The relative affinity of a species for the different categories were fuzzy coded from 0 (no affinity for the category) to a maximum value of 1 (meaning the species specializes solely in one category), to account for the capacity of some species to feed on different types of resources. We then used this information to calculate community-weighted mean values (CWMs—representing average trait values weighted by species abundances; Lavorel et al., 2008). An increased CWM for a given category indicates an increased relative abundance of the main feeding traits associated with that category in the community (Frainer & McKie, 2015).

2.11 | Data analysis

We constructed linear mixed effect models (LMM) to assess variation in univariate response variables, including measures of abundance, diversity and biomass of biota (fungi and shredders), benthic invertebrate feeding group CWMs, and individual abiotic variables (temperature, discharge, etc.). In line with our 'split-plot' experimental design (Figure 1), we fitted whole-channel identity (our experimental main plots) and subchannels nested within whole channels (our subplots) as random effects, to account for background variation among our experimental replicates. When fitting the model to the algal biomass accrual data, tile identity was also specified as a random factor nested within subchannels. Fixed effects comprised the drought treatment, tested using whole channels as replicates, and the habitat patchiness and enhanced connectivity treatments, which were tested using subchannels as replicates. Random effects were estimated with restricted maximum likelihood (REML), as this is robust to the slight imbalance in our data arising from the loss of some replicates (e.g tile or litterbag; Quinn & Keough, 2002). As part of REML estimation, the *df* for each fixed effect tested were also estimated, based on Kenward–Roger's approximation (Kenward & Roger, 1997). Variation explained by the random factors is reported as supplementary information (Tables S2.1, S2.3, S3.2, S3.4, S4.1, S4.2). Data were log- or square root-transformed when necessary to meet assumptions of normality and equality of variances. LMMs were tested using *lme4* (Bates, Maechler, Bolker, & Walker, 2015) and *lmerTest* (Kuznetsova, Bruun Brockhoff, & Bojesen Christensen, 2016), implemented in R v.3.5.1.

Fungal and leaf-shredder community data were first projected using non-metric multidimensional scaling (nMDS), followed by permutational multivariate analyses of variance (PERMANOVA) and permutational analyses of multivariate dispersions (PERMDISP), all implemented using the *vegan* package (Oksanen et al., 2015) based on Bray–Curtis dissimilarities. PERMANOVA was used to describe differences in means (i.e. centroids of the group communities) and PERMDISP to describe differences in dispersion (community heterogeneity) among our treatments and their interactions. For PERMANOVA and PERMDISP, we used the argument *strata* from the *adonis* function to account for spatial autocorrelation among replicates within subchannels (vegan R package; Oksanen et al., 2015). However, we were unable to use the *strata* argument to specify the nested structure of our random effects in the full hierarchical (split-plot) model. Instead, we analysed data for the two flow treatments (constant flow vs. drought) separately to assess interactions between habitat connectivity and spatial arrangement of resources and compared the results post hoc. In additional analyses, we assessed the effect of drought pooling across the other treatments. Although these analyses were not fitted using our complete split-plot model, we include them to support the nMDS ordination plots

in describing patterns in community composition. The *df* varied between analyses depending on the number of replicates included (arising from losses of a few litterbags or the absence of invertebrates from some replicates).

Indicator species (IS) analysis in the R package *indicspecies* (De Cáceres & Legendre, 2009) was used to describe which species were associated with community changes among the experimental treatments. We used the point-biserial correlation coefficient (r_{pb}) to indicate the strength of association between a taxon and the experimental treatment (De Cáceres & Legendre, 2009). Effects of the experimental treatments on the relative abundances of fungal and shredder taxa were assessed using *t* tests. Relationships between leaf-shredding invertebrate abundances and fungal abundances, richness, diversity, evenness and biomass from the coarse bags were assessed using linear models, with data pooled at the subchannel scale (dry vs. constant flowing only).

3 | RESULTS

3.1 | Environmental variables

The drought treatment affected all environmental variables, except turbidity and suspended chlorophyll *a* concentration (Table S2.1). The sum of degree days above zero were similar between the whole channels, both prior to the flow manipulation and during the post-recovery period (Table S2.3). However, during the flow manipulation period, daily mean temperature was marginally higher (0.38°C) in the control than dried whole channels (Table S2.2), as was degree day accumulation (constant flow [F]: 105.31 ± 0.44; drought [D]: 102.97 ± 0.47). At the subchannel scale, discharge in dried subchannels was significantly lower than that in the constant-flowing subchannels (Figure S2.1; Table S2.3) during the flow manipulation, but did not differ significantly between control and dry subchannels during the pre-disturbance and recovery periods. Discharge was marginally higher (16% on average) when litterbags were evenly spaced during the pre-disturbance and drying periods, but in the constant-flowing subchannels only (Figure S2.1; Table S2.3). Dissolved oxygen was not affected by any of the treatments (Tables S2.1 and S2.2).

3.2 | Biotic responses

3.2.1 | Fungal communities from the coarse bags

We identified a total of 193 fungal taxa. Fungal communities were dominated by Ascomycota (96%), Basidiomycota (3.5%), Chytridiomycota, Glomeromycota and Zygomycota (≈0.6% altogether). The ascomycetes *Clavariopsis* sp., *Lemonniera* sp., *Flagellospora* sp. and a further unidentified species were the most prominent taxa, with their cumulative relative abundances reaching 97% in some litterbags (Figure S3.1). Community composition characterized at the OTU level was not affected by drought overall (PERMANOVA: $F_{1,141}$ = 0.95; p > .05; PERMDISP: $F_{1,141}$ = 0.08; p > .05; Figure S3.2), though differences in the relative abundances of some fungal phyla and classes were detected. The classes Dothideomycetes and Pucciniomycetes were more abundant in drought-affected channels, while Monoblepharidomycetes and Ustilaginomycetes were more abundant in constant-flowing channels (Figure 3a; Figure S3.2). Interestingly, taxa associated with the constant-flowing subchannels were typical aquatic fungi (e.g. *Kappamyces* sp. and the Monoblepharidales family), while a terrestrial saprotrophic fungus, *Mortierella* sp., was associated with the drought treatment (IS analysis, Table S3.1).

Enhanced connectivity increased the dissimilarity of fungal communities between drought and control channels (PERMANOVA: $F_{1,68}$ = 2.04; R^2 = .028; p = .047; Figure S3.3), and also tended to

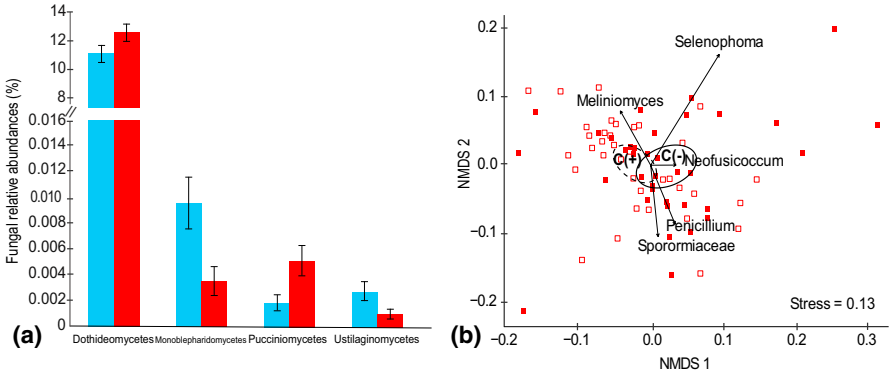

FIGURE 3 Effects of drought on fungal communities from the leaf litter: (a) relative abundances (mean ± *SE* per litterbag) of fungal classes under the constant flowing (blue bars) and drought (red bars) treatments; (b) an non-metric multidimensional scaling (nMDS) ordination of fungal communities encountered in the drought treatment only (litterbag n = 72; associated stress = 0.13), with the enhanced connectivity treatment overlaid (plain symbols: without enhanced connectivity (C(−)); open symbols: with enhanced connectivity (C(+))). The ordination plot further includes the 95% confidence intervals of the centroids for the enhanced (dotted lines) and non-enhanced (solid lines) connectivity treatments, and a biplot showing associations with the best-fitting fungal taxa. The nMDS ordination of fungal communities found only in the constant-flowing treatments is available in Figure S3.6a

increase community dispersion, with this result near significance at the 5% level (PERMDISP: $F_{1,70}$ = 3.74; p = .057). The Dothideomycetes genus *Neofusicoccum* was most associated with communities in the ambient connectivity channels (Figure 3b). A near-significant interaction between habitat patchiness and enhanced connectivity was also apparent (PERMANOVA: $F_{1,68}$ = 2.07; R^2 = .028; p = .056; Figure S3.4), whereas communities in evenly spaced but not aggregated litterbags differed between the connectivity treatments.

Fungal biomass was significantly higher in aggregated litterbags (by 10.76%; $F_{1,12}$ = 6.13; p = .029) and in litterbags not subjected to enhanced connectivity ($F_{1,12}$ = 13.04; p = .004). Fungal biomass was also affected by a three-way interaction between habitat patchiness, drought and enhanced connectivity ($F_{1,12}$ = 10.80; p = .007). Enhanced connectivity reduced fungal biomass across subchannels with evenly spaced habitats under the constant-flow treatment (Figure 4a). The lowest levels of biomass observed overall were in the subchannels with evenly spaced detrital habitats within the drought channels (Figure 4a).

There were no differences in fungal richness, diversity or evenness according to the any main treatment effect or interactions (all F < 3.53; all p > .09; Table S3.2). However, fungal taxa richness decreased as leaf-shredding invertebrate abundances increased in the coarse bags in constant flow (R^2 = .36; p = .04; Figure 4b) but not drought-affected channels (R^2 = .006; p = .81; Table S3.3).

3.3 | Leaf-shredding invertebrate assemblages from the coarse bags

Leaf shredders retrieved from the litterbags comprised of 10 taxa, with *Asellus aquaticus* (Isopoda: Asellidae) and *Nemoura flexuosa* (Plecoptera: Nemouridae) dominating (31.6% and 31.5% of the total number of individuals respectively). Community composition was not affected by drought overall (PERMANOVA: $F_{1,209}$ = 1.61; p > .05; PERMDISP: $F_{1,209}$ = 0.42; p > .05). However, differences in the abundances of some taxa were detected, with *Nemoura avicularis* (Plecoptera: Nemouridae) and Limnephilidae (Trichoptera) more abundant in the drought than constant-flowing channels (t_{125} = 3.13; p = .002; t_{160} = 2.94; p = .004 respectively; Figure 5a; Table S3.4).

In the drought-affected channels, enhanced connectivity significantly affected shredder community composition (PERMANOVA: $F_{1,101}$ = 2.57; R^2 = .024; p = .032; Figure 5b). Communities subjected to enhanced connectivity were dominated by *Taeniopteryx nebulosa* (Plecoptera: Taeniopterygidae) while Limnephilidae were more associated with litterbags in channels with ambient connectivity (Figure 5b; IS analysis, Table S3.4). There were no differences in leaf-shredder diversity, evenness or overall abundance among the treatments (all F < 3.53; all p > .09; Table S3.5), though there was a trend for enhanced connectivity to increase shredder biomass in the drought-affected channels (D:C(–): 4.61 ± 1.19; D:C(+): 21.44 ± 4.32 mg) not significant at the 5% level ($F_{1,12}$ = 3.53; p = .08).

3.3.1 | Benthic invertebrates

Post-drought, the shredder CWM was 1.65 times greater in dry than in constant-flowing subchannels (CWM: D: 0.28 ± 0.012; F: 0.17 ± 0.011; Table S3.6). Two-way interactions between drought and habitat patchiness (Table S3.6) were apparent for both scraper and predator CWMs. The scraper CWM was higher in channels with evenly spaced than aggregated habitats under constant flowing but not drought conditions (Figure S3.5). The predator CWM was higher in constant-flowing channels with aggregated habitat patches and in dry channels with evenly spaced habitat patches (Figure S3.5). By the end of the recovery period, neither the shredder nor scraper CWMs varied among the experimental treatments (Table S3.7) but the predator CWM remained higher in channels with evenly spaced than aggregated habitats (CWM: A: 0.21 ± 0.0043; E: 0.23 ± 0.0045;

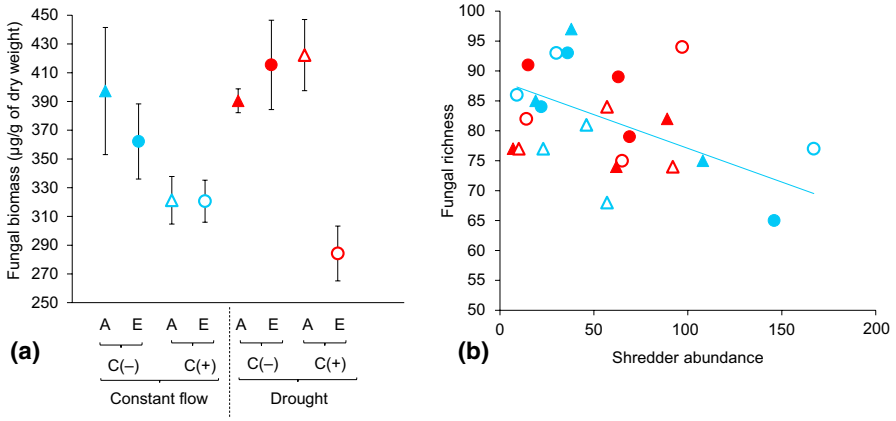

FIGURE 4 Effects of drought, habitat patchiness and enhanced connectivity on (a) fungal biomass (based on mean ± *SE* ergosterol concentration pooled at the subchannel scale) and (b) the relationship between fungal richness and leaf-shredding invertebrate abundance pooled at the subchannel scale. The fungal richness–invertebrate abundance relationship was only significant under constant flow, which is represented by the blue line (y = 88.33 – 0.11 × x). Constant flow: blue symbols; drought: red symbols; A: aggregated litterbags—triangles; E: evenly spaced litterbags—circles; C(–): without enhanced connectivity—plain symbols; C(+): with enhanced connectivity—open symbols

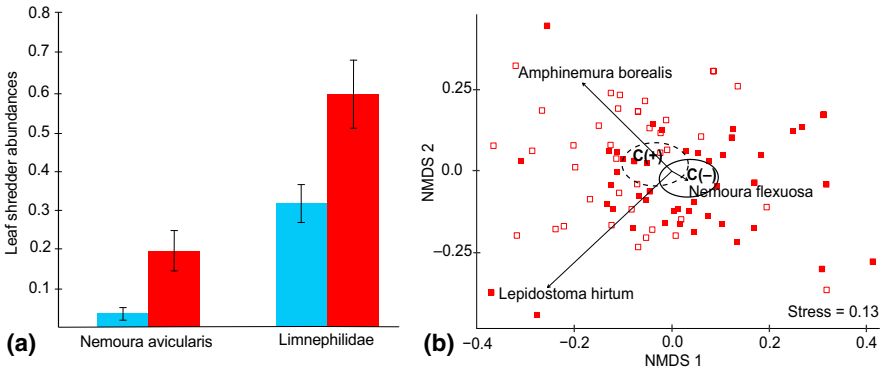

FIGURE 5 Effects of drought on leaf-shredding invertebrates from the leaf litter: (a) abundance (mean ± *SE* per litterbag) of the selected shredder taxa under the constant flowing (blue bars) and drought (red bars) treatments; (b) an non-metric multidimensional scaling (nMDS) ordination of shredder communities encountered in the drought treatment only (litterbag n = 105; associated stress = 0.13), with the enhanced connectivity treatment overlaid (plain symbols: without enhanced connectivity (C(−)), open symbols: with enhanced connectivity (C(+))). The ordination plot further includes the 95% confidence interval of the centroids for the enhanced (dotted lines) and non-enhanced (solid lines) connectivity treatments, and a biplot showing associations with the best-fitting shredder taxa. The nMDS ordination of shredder communities found in the constant-flowing treatment only is in Figure S3.6b

Table S3.7). Neither the deposit feeder nor filterer CWMs were affected by any of the treatments at either sample date (Table S3.7).

3.4 | Ecosystem functioning

3.4.1 | Algal standing stocks

Algal standing stocks were significantly affected by drought (F: 3.18 ± 0.088; D: 0.91 ± 0.044 mg/m^2; LMM: $F_{1,4.02}$ = 61.41; p = .001) and varied over time (Figure 6a; LMM: $F_{5,1,181.72}$ = 548.14; p < .001). Additionally, there were significant two-way interactions between drought and time, and between enhanced connectivity and time (LMM: $F_{5,1,183.83}$ = 425.44; p < .001 and $F_{5,1,183.83}$ = 6.38; p < .001 respectively; Figure 6a). A three-way interaction between drought, habitat patchiness and enhanced connectivity had a significant effect on algal standing stocks (LMM: $F_{1,12.03}$ = 6.38; p = .030; Figure 6b). At the end of the drying period, algal standing stocks were 33.3% lower in the drought-affected than control channels (Figure 6a). Enhanced connectivity increased algal standing stocks regardless of habitat patchiness in the drought treatment, but decreased standing stocks in subchannels with evenly spaced habitats under constant flow (Figure 6b). Overall, the highest levels of algal standing stocks observed in dry subchannels were observed in those with evenly spaced habitat and subjected to enhanced connectivity (Figure 6b).

3.4.2 | Decomposition of organic matter

Drought reduced litter decomposition in the coarse bags by a factor of 1.20 ($F_{1,4}$ = 33.81; p = .004; Figure 7a) but had no significant effects on litter decomposition in fine bags, or on the tensile strength of cotton strips. No effect of habitat patchiness or enhanced connectivity in these variables were detected immediately after the

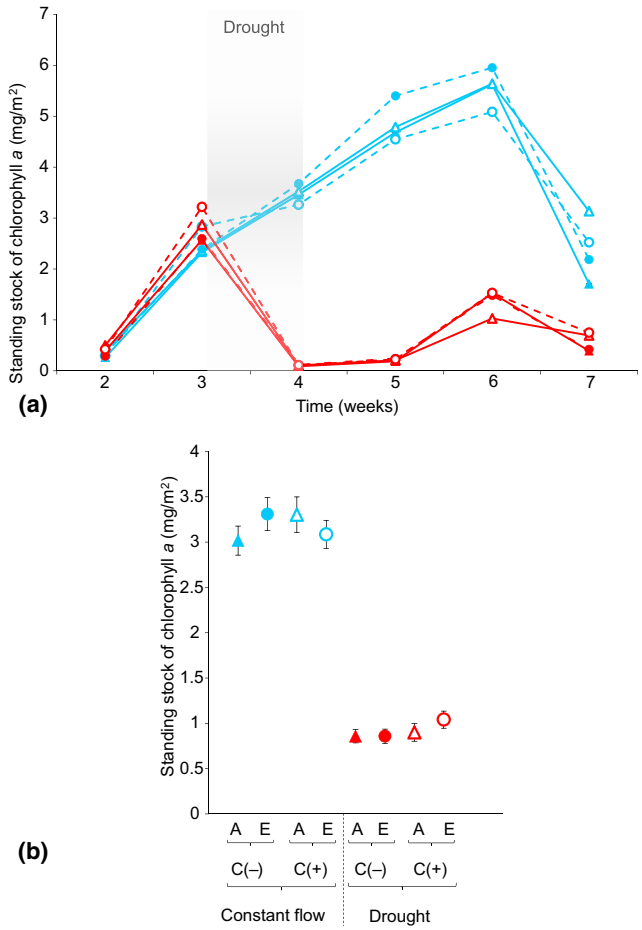

FIGURE 6 (a) Standing stocks of chlorophyll *a* (mean ± *SE*) over time and (b) effects of habitat patchiness (A: aggregated litterbags [triangles] vs. E: evenly spaced litterbags [circles]), drought (constant flow in blue vs. drought in red) and enhanced connectivity (C(−): without enhanced connectivity [plain symbols]; C(+): with enhanced connectivity [open symbols]) on algal standing stocks averaged across sampling dates (mean ± *SE*)

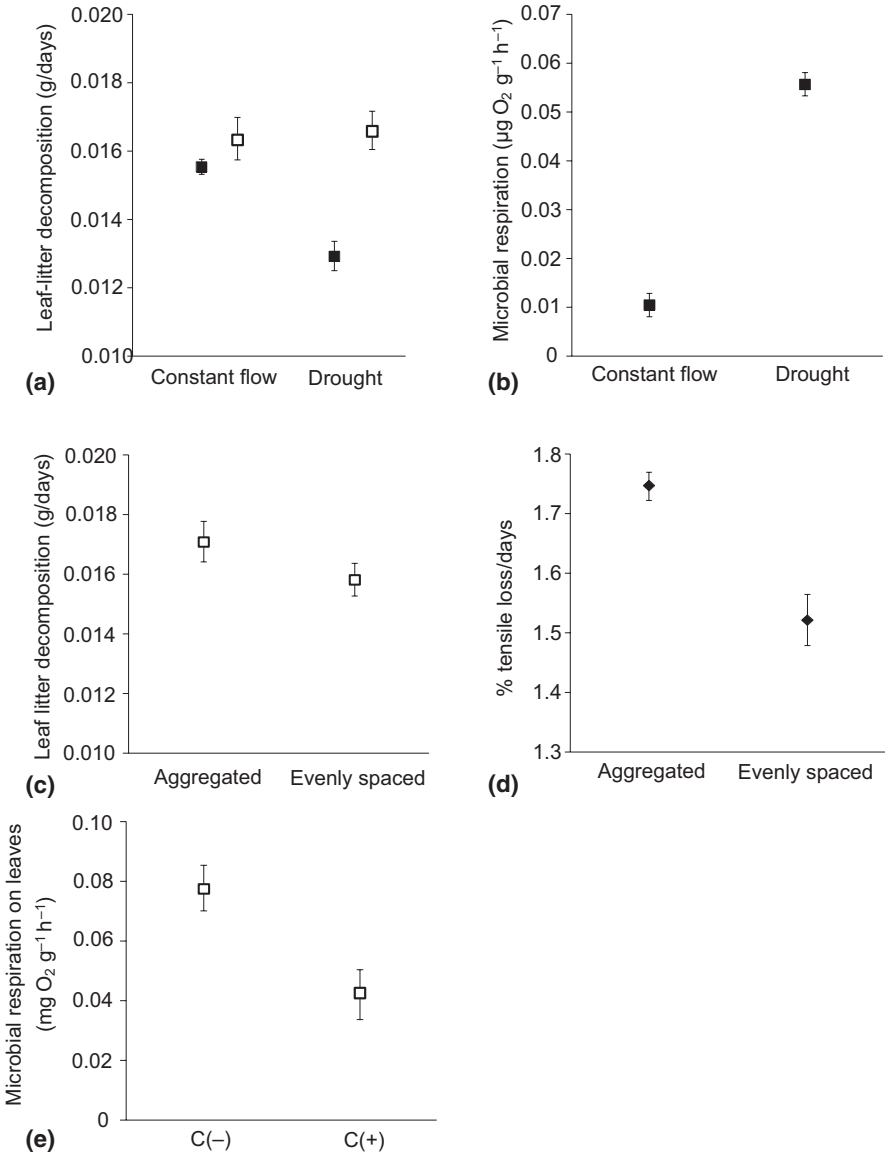

FIGURE 7 Effects of drought at the end of the post-recovery period on (a) decomposition rates (mean ± *SE*) in coarse (solid symbols) and fine (open symbols) bags and on (b) microbial respiration (mean ± *SE*) on cotton strips from within the coarse litterbags. Effects of habitat patchiness (aggregated vs. evenly spaced litterbags) on (c) litter decomposition rates in fine bags and (d) the percent of tensile strength loss of the cotton strips buried in the subchannel sediments. (e) Effects of enhanced connectivity treatment on microbial respiration from the leaves enclosed in the fine bags (C(–): without enhanced connectivity; C(+): with enhanced connectivity)

drought period ended. However, at the end of the experiment, litter decomposition in the fine bags and tensile strength loss of buried cotton strips were 8% and 14.7% higher, respectively, in channels with aggregated than even habitats (both $F_{1,11.99} > 6.73$; $p < .024$; Figure 7c,d). Tensile strength of buried cotton strips was also lowered at the end of the experiment by the combination of drought and enhanced connectivity, though this result was not significant at the 5% level (two-way interaction D:C: $F_{1,11.99} = 3.83$; $p = .07$; Figure S4.1).

3.4.3 | Microbial respiration

No effects of any of the treatments on microbial respiration were detected immediately post-drought. However, by the end of the experiment, microbial O_2 consumption of the surface cotton strips had increased by a factor of 5.34 in channels exposed to drought ($F_{1,4} = 30.1$; $p = .005$; Figure 7b). No other main effects or interactions were significant (all $p > .08$; Table S4.2). Respiration of microbes from leaves in fine bags was affected by the connectivity treatment, with respiration rates 1.85 times lower under enhanced compared with ambient connectivity ($F_{1,12} = 5.97$; $p = .03$; Figure 7e).

4 | DISCUSSION

Our results highlight the profound impacts that even a short period of drying can have on multiple aspects of benthic structure and function in boreal streams, with many of these impacts persisting at the end of the experiment when water had been available for weeks after the drought. Notably, two basal ecosystem processes in freshwater food webs, algal biomass accrual and leaf decomposition mediated by invertebrates, remained suppressed at the end of the recovery period, while microbial respiration rates were elevated. Drought also caused clear shifts in the community composition of both fungi and invertebrates. Our

spatial manipulations modified the effects of drought to a small extent (e.g. the slightly elevated algal biomass accrual observed in drought-affected channels with evenly spaced habitats and enhanced connectivity), highlighting the potential for spatial dynamics associated with habitat patchiness and connectivity with a regional species pool to contribute to ecosystem stability. Such effects were minor relative to the strong impacts of drying, but might accumulate in importance over larger spatiotemporal scales than studied here. However, overall our experiment indicates that the potential for functional recovery of boreal stream ecosystems following short late summer droughts is likely to be very low.

4.1 | Drought effects on communities and processes

4.1.1 | Drought effects on biotic communities

Our results support previous findings that terrestrial fungi increase in importance during drying, as the activity and diversity of aquatic fungi decline (Chauvet et al., 2016; Mustonen et al., 2016). This is exemplified by the association of *Mortierella* sp., a terrestrial saprotroph Mucoromycota in decaying leaves (Kjøller & Struwe, 2002) with the drought-affected channels, and concurrent declines in several freshwater Ascomycota. In contrast with fungi, leaf-shredding invertebrates were little affected by drought, indicating a high degree of resistance during the dry period and/or rapid recovery thereafter. None of our shredder species are recorded as having a diapause or other strategy for resisting drought (Tachet et al., 2010). Rather, the limited effects of drought on shredders are likely to reflect their capacity to take advantage of refuges provided where moisture is retained, for example in interstices within the cobble substrate, or within the leaf packs (Vadher, Leigh, Millett, Stubbington, & Wood, 2017; Williams & Hynes, 1977). Alternatively, shredders might have moved to pools formed during the drought (Bogan et al., 2015; Boulton, 1989), especially as our shredder assemblages were dominated by crawling species (Figure 4; Tachet et al., 2010). Indeed, shredder feeding traits increased in dominance in dry channels immediately after water flows resumed, suggesting that shredders more than other feeding groups became concentrated in such refuge habitats during the drying phase.

4.1.2 | Drought effects on litter decomposition

Despite the recovery of leaf-shredding invertebrates by the end of the experiment, litter decomposition in the coarse bags remained lowered in the drought-affected channels, similar to some previous observations (Bruder, Chauvet, & Gessner, 2011; Leberfinger, Bohman, & Herrmann, 2010; Schlief & Mutz, 2009). Notably, for the drought treatments, leaves in the middle of the coarse bags were often characterized by blackened areas, indicative of anaerobic decomposition processes (Bruder, Salis, McHugh, & Matthaei, 2016). Anoxic conditions may directly reduce the rates of decomposition by excluding shredders from some portion of the litterbags (Sponseller & Benfield, 2001), while anoxic decomposition processes can decrease litter palatability (Bärlocher, 1992a; Suberkropp, Arsuffi, & Anderson, 1983) and the activities of litter-associated hyphomycetes (Medeiros, Pascoal, & Graca, 2009). Overall, those results support the idea that high mobility and the use of refugia by shredders combined with reduced activity—but not mortality—of fungal decomposers are mechanisms that help to restore the levels of decomposition comparable to those observed under constant flow and maintain litter decomposition after the drought (Bruder et al., 2011; Langhans & Tockner, 2006). We did not observe any corresponding decrease in decomposition nor any evidence of blackened leaves in the fine bags. However, the much smaller quantity of litter in these bags relative to the coarse bags is likely to have resulted in more rapid drying in the drought-affected channels, limiting potential for anoxic decomposition processes to develop. Implications of the impacts of drought on litter decomposition (e.g. Abril, Muñoz, & Menéndez, 2016; Bruder et al., 2011; Shumilova et al., 2019) are worthy of further investigation, given the key role decomposition plays in C and nutrient cycling (Gessner, Chauvet, & Dobson, 1999; Gessner et al., 2010).

4.1.3 | Drought effects on algal biomass accrual

In contrast with fungal biomass accrual, algal biomass accrual was heavily impacted by drought. This is consistent with the known vulnerability of benthic algae to water loss, as illustrated elsewhere in both field (e.g. Stanley, Fisher, & Jones, 2004; Timoner, Acuña, Von Schiller, & Sabater, 2012) and mesocosm studies (e.g. Acuña, Case Ilas, Corcoll, Timoner, & Sabater, 2015), and might also reflect the greater exposure of algae biofilms growing on our tile surfaces, compared with fungal mycelia embedded within litter patches. However, unlike in previous studies (e.g. Timoner, Buchaca, Acuña, & Sabater, 2014), algal recovery following the restoration of flow was slow, with standing stocks remaining very low in dry channels at the end of the experiment. These findings suggest that even short dry spells occurring later in the summer or autumn might potentially set back algal growth in boreal streams to such an extent that there is insufficient time for recovery, prior to the seasonal dieback that results from environmental constraints in this region (e.g. low light and cold temperatures). Such seasonal dieback is evidenced in our experiment by the downturn in algal standing stocks across all treatments at the last sample date. There was evidence that greater spatial connectivity might favour greater recovery in the functioning of algal biofilms, with the enhanced connectivity treatment associated with slightly elevated algal standing stocks in drought-affected channels on the final sample date. This was not associated with any change in the relative abundance of scraper traits in the benthic assemblages of these channels, but might instead reflect the addition of new algal propagules attached to invertebrates added in the enhanced connectivity treatment (Table S3.7). Regardless of the underlying cause, the effect of enhanced connectivity was small relative to the main

effect of drought, and was insufficient to drive significant recovery in algal standing stocks, prior to autumn biofilm dieback.

Algal biomass provides a labile C source for stream consumers that is rich in nutrients including polyunsaturated fatty acids (e.g. Brett et al., 2017; McCutchan & Lewis, 2002). Accordingly, the limited resistance and recovery of periphyton to drought evident here has a potential to impact subsequent secondary production, even in very heterotrophic systems, as suggested by previous experimental work (Ledger, Brown, Edwards, Milner, & Woodward, 2013; Ledger, Edwards, Brown, Milner, & Woodward, 2011). Furthermore, algae interact with heterotrophic microorganisms, with exudates of labile compounds known to stimulate microbial activity and detritus decomposition (Brett et al., 2017; Halvorson, Scott, Entrekin, Evans-White, & Scott, 2016; McCutchan & Lewis, 2002). Indeed, in a long-term stream study, reduced bacterial productivity following floods that destroyed algal biofilms was associated with the reduced availability of algal exudates (Olapade & Leff, 2005). The failure of algal biofilms to recover following drought might similarly have ongoing impacts on heterotrophic microbes, even if a transient increase in leaching of labile compounds from dead biofilms following drought might briefly stimulate microbial activity (consistent with the higher respiration rates observed in our study, e.g. Suberkropp, Gulis, Rosemond, & Benstead, 2010). In boreal regions, droughts that reduce instream production of low molecular weight C during summer photosynthesis might be particularly important for the functioning of streams during the region's long, dark winters, given evidence from one boreal catchment that respiration of heterotrophic microbes during the winter is strongly limited by availability of labile C rather than nutrients (Burrows, Laudon, McKie, & Sponseller, 2017).

4.2 | Role of spatial structure and connectivity

Our spatial manipulations affected multiple response variables, and in some cases modified the effect of drought to a small extent. However, effect sizes associated with most of our spatial treatments were generally much lower than those of drought. The relevance of habitat patchiness to different organism groups depends on their scale-dependent movement and activity patterns (Levin, 1992; Wiens, 1989). In our experiment, habitat patchiness did not seem to be important for leaf-shredding invertebrates, or invertebrate-mediated decomposition, but did affect both fungal biomass and microbially mediated ecosystem processes, that is, litter decomposition in fine bags and organic matter decomposition in the sediments. Previous studies have suggested that microbes are not strongly dispersal limited (Giller et al., 2004; Kivlin et al., 2014), attributed to the effectiveness of transport agents such as stream flow (Bärlocher, 1992b) and the macroinvertebrates themselves (Bärlocher, 1981; Chauvet et al., 2016), and it is possible that if we had maintained our experiment over a longer time period, ongoing propagule production and dispersal might have obscured some of the effects observed here. Nevertheless, the positive response of microbially mediated detrital decomposition to greater habitat aggregation was consistent both above and within the stream substrate, and might reflect local entrapment and build-up of fungal spores and/or conidia among the litterbags (Cornut, Elger, Lambrigot, Marmonier, & Chauvet, 2010; Gessner & Chauvet, 1994), favouring more rapid microbial conditioning and decomposition (Bärlocher, Nikolcheva, Wilson, & Williams, 2006; Bärlocher, Seena, Wilson, & Williams, 2008). Habitat patchiness also interacted with drought to influence the relative abundance of both scraper and predatory invertebrate traits. Notably, evenly spaced habitat patches were associated with an increased dominance of scrapers in the control but not drought-affected channels in the benthic communities sampled immediately post-stressor, which might have resulted in increased grazing pressure and hence the lowered algal biomass accrual observed in these channels during this period (week 5, Figure 6a).

Enhanced connectivity was associated with shifts in community composition both for fungi and shredders in the litterbags in the drought-affected channels at the end of the experiment. This suggests that the enhanced connectivity treatment not only introduced new shredder individuals but also introduced new fungal propagules (attached to invertebrate bodies or carried inside their digestive tracts), and that the preceding drought increased the opportunities for these individuals and propagules to establish and shift community composition. Alternatively, changes in fungal communities might reflect differences in the feeding preferences of the shredder communities established following the enhanced connectivity treatment (Arsuffi & Suberkropp, 1989; Bundschuh et al., 2011). Enhanced connectivity further caused reductions in fungal biomass, which is in line with previous laboratory studies showing that connectivity with a regional species pool reduced local microbial biomass (de Boer, Moor, Matthiessen, Hillebrand, & Eriksson, 2014; Matthiessen & Hillebrand, 2006). In our study, reduced fungal biomass was associated with a trend for increased shredder biomass under the enhanced connectivity treatment (possibly reflecting addition of individuals of some of larger shredder taxa, including the stonefly *T. nebulosa*, caddisfly *Lepidostoma hirtum* and isopod crustacean *A. aquaticus*, Table S1.2) which is likely to have increased grazing pressure on fungi. Overall, these results point towards the potential for invertebrates to control the structure and functioning of fungal biofilms from the top-down (Gardeström, Holmqvist, Polvi, & Nilsson, 2013; Gessner et al., 2010). There was no relationship between invertebrates and fungi under the drought treatment, especially in the aggregated habitats where fungal biomass strongly increased, supporting previous research showing that drought alters the dynamics of food webs (Ledger, Brown, Edwards, Hudson, et al., 2013; Ledger, Brown, Edwards, Milner, et al., 2013).

5 | CONCLUSIONS

The boreal region is the world's second largest biome covering 12% of the Earth's surface (Baldocchi et al., 2000), and current climate predictions suggest substantial changes in the seasonality and

quantity of precipitation (rain, snow) which together with increases in the water demands of terrestrial vegetation will strongly influence the hydrological dynamics of streams (Teutschbein, Grabs, Karlsen, Laudon, & Bishop, 2015; Teutschbein et al., 2017). Importantly, in the boreal zone, complete drying often occurs mostly in the headwaters (Schindler et al., 1996) and our understanding of how these communities recover remains poor. Compared with more hydrologically connected habitats lower in the river networks, which are both less prone to dry out and more likely to have a supply of recolonizing organisms originating from upstream, headwaters are more likely to be dependent on recolonization from outside the immediate catchment (Bogan et al., 2015; Elmqvist et al., 2003). Our experiment demonstrates the potential for even shorter term hydrological disturbances to have extended consequences for ecosystem processes underpinning C and N cycles in headwater boreal streams, especially when occurring late in the summer when the time available for recolonization of key organisms prior to the winter is limited.

Summer 2018 saw record drought across Scandinavia affecting social-ecological systems with large fires (including north of the Arctic Circle; SMHI, 2018) and bans on fishing (SverigesRadio, 2018). This highlights the need for an improved understanding of the key structural and functional attributes that help underpin the potential adaptive capacity and resilience of ecosystems to deal with shifting disturbance regimes under global change, and which if undermined might result in the reorganization of ecosystems into distinctly different regimes that often jeopardize important ecosystem functions (Angeler & Allen, 2016; Angeler et al., 2019; UNEP, 2005; Urban et al., 2008). Increasing the ecological connectivity of habitats and ecosystems has been advocated as one concrete management measure for enhancing the resistance and resilience of degraded ecosystems, and preventing undesirable regime shifts (Angeler et al., 2014; Suding, Gross, & Houseman, 2004). However, the overwhelming impacts of drought appear to limit the efficacy of increased ecological connectivity for enhancing recovery of boreal stream ecosystems, at least at the observational scale of our study.

ACKNOWLEDGEMENTS

The authors are grateful to the staff from the Kainuu Fisheries Research Station, along with Anna-Leena Taskinen, Leif Väisänen, Tessel Lagerwerff, Dimitrios Rados and Elodie Chapurlat for assistance during the experiment. This work was supported by grants from the Swedish Environmental Protection Agency and the Swedish Agency for Marine and Water Management to R.K.J. and B.G.M. (project WATERS, Dnr 10/179) and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS) to B.G.M. (project DESTRESS, Dnr 2014-886). Additional funding was supplied from a PhD student grant from the Department of Aquatic Sciences and Assessment (SLU, Uppsala) to A.T., and from the University of Oulu Graduate School (UniOGS) to R.S., the Academy of Finland (AKVA research program) to T.M. and the Natural Resources Institute Finland (Luke) to A.H. Comments by anonymous referees were appreciated and improved the quality of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Swedish National Data Service at https://doi.org/10.5878/jrn0-0520.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Truchy A, Sarremejane R, Muotka T, et al. Habitat patchiness, ecological connectivity and the uneven recovery of boreal stream ecosystems from an experimental drought. *Glob Change Biol*. 2020;26:3455–3472. https://doi.org/10.1111/gcb.15063